

PHENOTYPIC VARIATION OF RARE AND WIDESPREAD SPECIES OF *PLANTAGO*

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The notion that populations of restricted species are genetically depleted is based on population models which show rapid gene fixation because of genetic drift and selection in small populations (Rothstein, 1973; Babbel & Selander, 1974). If this is true, populations of rare species should show less phenotypic variability in the field than populations of widespread, closely related species due to lower amounts of genetic variation. With the exception of the genus *Becium*, in which leaf dimensions of a widespread species were shown to be more variable than those of a restricted species (Wild & Heyting, 1966), this assumption has not been tested for plants. In order to test further this assumption, I examined the phenotypic variability of reproductive characters within populations of *Plantago* (Plantaginaceae) species, commonly known as plantains, in relation to the distributions of the species. In addition, herbarium specimens were examined for these species to gain a rough measure of the total phenotypic variability found throughout the ranges of the species. Would widespread species show more phenotypic variability than restricted species?

The genus *Plantago* is well suited for such a comparison of geographical distribution and phenotypic variability; species of *Plantago* vary from endemic species with highly restricted distributions and specialized habitat requirements to cosmopolitan species that occupy a wide variety of habitats. However, species of *Plantago* share the same floral characters associated with wind-pollination (Primack, 1978a) and the same fruit type, a circumscissile capsule.

MATERIALS AND METHODS

Data from herbarium material

Reproductive characters were determined for *Plantago* species using herbarium specimens. The range, habitat, and longevity for each species are presented in Table I. Species and individuals within populations show variation in four reproductive characters which have been used taxonomically and which collectively determine the total weight of seeds produced per plant, the seed yield (Primack, 1978b). In this study, species are contrasted for their variation in

these four characters. The following characters were measured: inflorescence number per plant (Infl.), capsule number per inflorescence (based on the inflorescence which is median in size) (Caps.), seed number per capsule based on a sample of at least three capsules (Seed no.), and the weight per seed based on a sample of at least ten mature seeds (Seed weight). An individual was ordinarily a single rosette on a shortened stem, though occasionally there was more than one rosette per stem. The herbarium specimens were picked at random from those available, and included specimens from throughout the distribution of the species. A detailed description of the way in which the herbarium specimens were evaluated is given elsewhere (Primack, 1976, 1978b, 1979). This sampling procedure considers only the overall variation of a species, not distinguishing between genetic and environmental components contributing to this variation and the underlying population structure of the species. Taxonomy follows Pilger (1937).

Mature seeds could not be obtained from every specimen. Consequently, the variation in weight per seed is not reported for every species. Many herbarium specimens contain some capsules which have already shed their seeds. However, this study did not involve actually counting each seed per plant, but rather involved measuring the four reproductive characters for each plant.

Data from field collections

Individual plants were collected randomly from populations of sixteen species of *Plantago* found in North America (see Primack, 1978b, for localities), and examined for the four reproductive characters. Seven species were perennials and nine were annuals. In four species (*P. eriopoda*, *P. tweedyi*, *P. cordata*, and *P. heterophylla*), the seeds were not mature at the time of sampling.

Statistical analysis

Coefficients of variation were calculated for each reproductive character in order to determine which species were the most variable. Species are grouped into five distribution classes according to available information on the extent of their geographical range (Table 1). Further investigation might show that particular species should be re-assigned to an adjacent distribution class. However, this classification system does separate out the most restricted and the most widely distributed species for comparison.

Both parametric and non-parametric correlation matrices were calculated for the coefficients of variation in order to determine: 1) if species which are variable for one character are likely to be variable for another character, and 2) if species which are particularly variable for a character based on herbarium specimens are also likely to be variable for that character based on population samples.

RESULTS

Relationship of range to the amount of phenotypic variation

Species show a wide variety of coefficients of variation using herbarium specimens, with some species being relatively invariable, while others are quite variable (Table 1). There is no obvious pattern of increasing variation with increasing distribution. If anything, species with restricted ranges seem to have more variation for seed number per capsule than species with larger ranges.

Similarly, species show a wide variety of coefficients of variation using population samples (Table 1). There is again no obvious pattern of increasing variation with increased distribution for three of the characters. There is a trend toward greater variation in capsule number per inflorescence in species with increased range. However, this observation must be treated cautiously because of the large variability of values within each distribution class.

In summary, the amount of phenotypic variation found within single populations and within the total species is not related to the range of the species.

Correlation analysis

The results of the parametric and non-parametric tests gave similar values and the same levels of significance. Consequently, only parametric tests are presented.

There is no correlation among species for their coefficients of variation using herbarium specimens (Table 2), except that species which are more variable for inflorescence number per plant are

Table 1. Coefficients of variation ($CV = (\text{standard deviation}/\text{mean}) \times 100$) for *Plantago* reproductive characters, based on population samples and herbarium samples. Species are arranged in classes of increasing range. Sample sizes (N) are the same for all characters within a species and sampling method except where listed separately in parentheses. Habitat and life span for each species given by Primack (1978b). Data from Primack (1978b).

Species	Distribution
Restricted distribution; specialized habitat requirements:	
<i>P. cordata</i>	E. North America
<i>P. macrocarpa</i>	W. coast of N. America
<i>P. tweedyi</i>	W. North America
<i>P. eriopoda</i>	North America
<i>P. sparsiflora</i>	S. E. United States
<i>mean</i>	
Somewhat restricted distribution:	
<i>P. bigelovii</i>	W. North America
<i>P. pusilla</i>	Central United States
<i>P. elongata</i>	W. North America
<i>mean</i>	
Occurring on part of a continent:	
<i>P. wrightiana</i>	S. United States
<i>P. hookeriana</i>	S. North America
<i>P. rhodosperma</i>	S. North America
<i>P. helleri</i>	S. Central United States
<i>P. heterophylla</i>	S. E. United States
<i>mean</i>	
Widespread within much of a continent:	
<i>P. aristata</i>	E. North America
<i>P. bellardi</i>	Mediterranean
<i>P. virginica</i>	North America
<i>P. rugelii</i>	E. North America
<i>P. amplexicaulis</i>	Mediterranean
<i>mean</i>	
Widespread; occurring in a variety of habitats or on two or more continents	
<i>P. patagonica</i>	Americas
<i>P. linearis</i>	Tropical Americas
<i>P. psyllium</i>	Cosmopolitan
<i>P. ovata</i>	Mediterranean, S. Asia
<i>P. major</i>	Cosmopolitan
<i>P. hirtella</i>	Americas
<i>P. depressa</i>	E. & Central Asia
<i>P. lanceolata</i>	Cosmopolitan
<i>P. maritima</i>	Northern Hemisphere
<i>P. coronopus</i>	Cosmopolitan
<i>mean</i>	

Herbarium Samples					Population Samples				
N	Infl.	Caps	Seed No.	Seed Weight	N	Infl.	Caps.	Seed No.	Seed Weight
20	40	44	28(19)	—	15	47	29	12	—
20	43	48	27	—	—	—	—	—	—
20	46	54	17	—	18	43	46	29	—
20	53	30	26	30(13)	19	50	51	—	—
14	66	33	20	—	19	29	20	19	22
	50	42	24	30		42	36	20	22
12	57	61	38	—	—	—	—	—	—
20	85	40	14	—	—	—	—	—	—
19	93	56	13	—	—	—	—	—	—
	78	52	21	—	—	—	—	—	—
20	97	35	0	—	20	59	46	0	11
15	72	79	0	—	19	44	29	9	16
20	62	58	0	—	20	75	31	3(19)	15(16)
20	123	46	0	—	20	64	56	3	23
20	92	47	23	26(11)	20	73	50	36(15)	—
	89	53	5	26		63	42	10	16
19	78	42	0	28(12)	18	35	50	13	23(17)
20	112	58	0	—	—	—	—	—	—
19	80	57	12	—	20	44	26	3	9
18	99	58	31	32(16)	20	43	47	15	20
17	106	72	9	—	—	—	—	—	—
	95	57	10	30		41	41	10	17
20	81	51	0	—	20	0	78	0	13(13)
20	86	55	0	—	—	—	—	—	—
20	123	45	0	—	20	90	36	9	20
20	111	48	0	—	—	—	—	—	—
19	43	74	34	30(16)	20	41	47	24	22
20	53	55	13	—	—	—	—	—	—
14	58	48	7	—	—	—	—	—	—
20	58	84	26	—	—	—	—	—	—
20	78	48	19	40(11)	20	87	41	24	23
20	85	83	28	29(10)	—	—	—	—	—
	78	59	13	33		54	50	14	20

significantly less variable for seed number per capsule. Generally, the fact that individuals of a species show a high degree of variation for one reproductive character does not mean that the species will be more or less variable for the other characters.

There is no overall correlation among species for the coefficients of variation using population samples, except that there was a significant positive correlation among species for the coefficients of variation for weight per seed and seed number per capsule (Table 2).

Correlation analysis was also used to determine if the species showing the most variation for a character using herbarium specimens are also the most variable using population samples. There was no significant correlation between the two sampling methods for inflorescence number per plant ($r = +0.36$, $n = 16$) and capsule number per inflorescence ($r = -0.09$, $n = 16$), but there was a significant correlation for seed number per capsule ($r = +0.68$, $n = 15$, $p < 0.01$). Not enough species were available to compare the variation of weight per seed using the two methods.

Considering that fifteen correlation coefficients are being reported, one significant correlation coefficient would be expected by chance. Since only three correlation coefficients out of fifteen are statistically significant and only two positively so, there appears to be at best a weak relationship between the amount of variation for pairs of characters and for the same character using the two methods.

DISCUSSION

Populations of restricted species may have more genetic variability than has previously been suspected. Restricted seed dispersal, nearest neighbor pollinations, and local adaptations to the environment may all contribute to a genetically heterogeneous population (Levin, 1977; Keeler, 1978). In this case, genetic differences might occur between sub-populations within the population. However, genetic variability may still not allow a population to persist if the environmental changes are beyond the physiological tolerances of the species (Meagher, Antonovics, & Primack, 1978).

The phenotypic variation found within a population is caused by both genetic differences among plants and differences in the immediate environment in which the plants are growing. This study has shown that populations of rare *Plantago* species do not contain less phenotypic variation than populations of common species. If one

Table 2. Correlation coefficients among species using coefficients of variation for inflorescence number per plant (I), capsule number per inflorescence (C), seed number per capsule (S), and weight per seed (W). Sample sizes are given in parenthesis.

For herbarium samples:

	C	S	W
I	-0.07 (28)	-0.55* (28)	-0.01 (7)
C	—	0.20 (28)	-0.06 (7)
S	—	—	0.06 (7)

For population samples:

	C	S	W
I	-0.31 (16)	0.18 (15)	0.21 (12)
C	—	-0.06 (15)	0.03 (12)
S	—	—	0.72* (12)

* $P \leq 0.01$

assumes that populations of rare species have less genetic variation than populations of common species, then these populations of rare *Plantago* species must have increased environmental variation in order to still have the same overall amounts of phenotypic variation as the common species. This does not seem likely. The equivalent phenotypic variability found in rare and common species probably indicates that populations of these *Plantago* species have similar amounts of genetic variation. If this is true, plant species may be rare more for historical and ecological reasons than for genetic reasons. Further studies comparing the amounts of variation in common and rare species should consider that the amount of variation that a species shows for one character gives no indication as to how much variation that species will show for other characters. Consequently, the results may be strongly affected by the choice of characters.

Rare species are often assumed to be prone to extinction since little genetic variation is available to respond to changes in the environment (see Drury, 1974), for a discussion of this point). However, the botanical evidence to confirm these assumptions is limited. This is surprising since plant species are well suited for answering genetic questions. Individuals of closely related rare and widespread species can be grown from seed under different sets of standard greenhouse conditions and directly measured for their amounts of genetic variability for morphological characters, as suggested by Stebbins (1942). Specific experimental designs for examining and testing differences between species in their amounts of genetic variability have been developed by Lewontin (1966) and Marshall and Jain (1968). In one study where this procedure has been used, the widespread species, *Stephanomeria exigua* ssp. *coronaria* (Compositae), showed more morphological variability than the restricted and recently derived species, *S.* "*Malheurensis*" (Gottlieb, 1973).

Another promising technique for comparing the genetic variability of rare and common species is electrophoresis to examine enzyme polymorphisms. In comparative studies, this technique has shown that populations of restricted species have less genetic variation than populations of widespread species in the genera *Stephanomeria* (Gottlieb, 1977) and *Lupinus* (Babbel & Selander, 1974). However, enzyme studies must be evaluated cautiously, because only a small part of the genome is being sampled and the technique may not be sensitive enough to separate out similar bands (Johnson, 1977). For example, enzyme studies failed to show differences between populations of *Typha* (Mashburn, Sharitz, & Smith, 1978) and sub-populations of *Veronica* (Keeler, 1978), where greenhouse studies of morphological and physiological characters had shown these units to be different genetically. Consequently, greenhouse studies may still be the most effective way to compare the genetic variability of rare and common species.

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